CHAPTER 7:
PATTERNS OF INVERTEBRATE DIVERSITY

RESULTS

Patterns of Invertebrate Alpha Diversity

General Patterns

A total of 254 different invertebrate families were detected during sampling in 1995 and 1996 combined, comprising 67% of the invertebrate families potentially occurring in the Lake Tahoe basin. Of the 254 families, 203 were observed in 1996 alone, including 17 families in the class Arachnida (spiders), 1 family in the class Chilopoda (centipedes), 2 families in the class Bivalva (bivalve molluscs), 5 families in the class Gastropoda (snails), and 180 families in the class Hexapoda (insects) (Appendix 9). These families were identified from a total of approximately 60 unique taxa detected per reach. Taxonomic richness was calculated in addition to family richness because of the large number of observations above the family level (approximately 10 per reach). The analysis of taxonomic and family richness was restricted to data collected in 1996 ($n = 56$ sample reaches) because of the significant inter-year differences observed in the taxonomic and family richness of invertebrates (see Chapter 3).

Taxonomic richness and invertebrate family richness were highly correlated (r = 0.978, $P < 0.001$), therefore only family richness was used to represent the diversity of all invertebrates. Family richness ranged from 31 to 83 families per reach ($\bar{x} = 49.9$, SE = 1.59). The 10 most frequently occurring invertebrate families consisted of a range of taxa, including spiders, beetles, flies, butterflies, leafhoppers, and ants (Fig. 43). These 10 families accounted for only 18.5% of all observations. Three typically speciose families occurred on every reach: Lycosidae (wolf spiders), Formicidae (ants), and Carabidae (carabid beetles). Four additional families had frequencies > 90%: Gnaphosidae (hunting spiders), Cicadellidae (leafhoppers), Phalangidae (daddy-longlegs), and Staphylinidae (rove beetles). The remaining 3 families varied in frequency from 80 to 90%, and consisted of Phoridae (humpbacked flies), Nymphalidae (brush-footed butterflies), and Sciaridae (dark-winged fungus gnats).

Environmental Relationships of Invertebrate Richness

Correlations

Invertebrate family richness was significantly correlated with 7 of the 22 environmental variables measured (Table 104). Invertebrate family richness was significantly negatively correlated with gradient and positively correlated with sinuosity, indicating a positive association with slow, windy stream reaches. The remaining 5 significant correlations were with vegetation variables: positive correlations with alder–willow, meadow, and lodgepole pine, and negative correlations with mixed conifer and large logs.
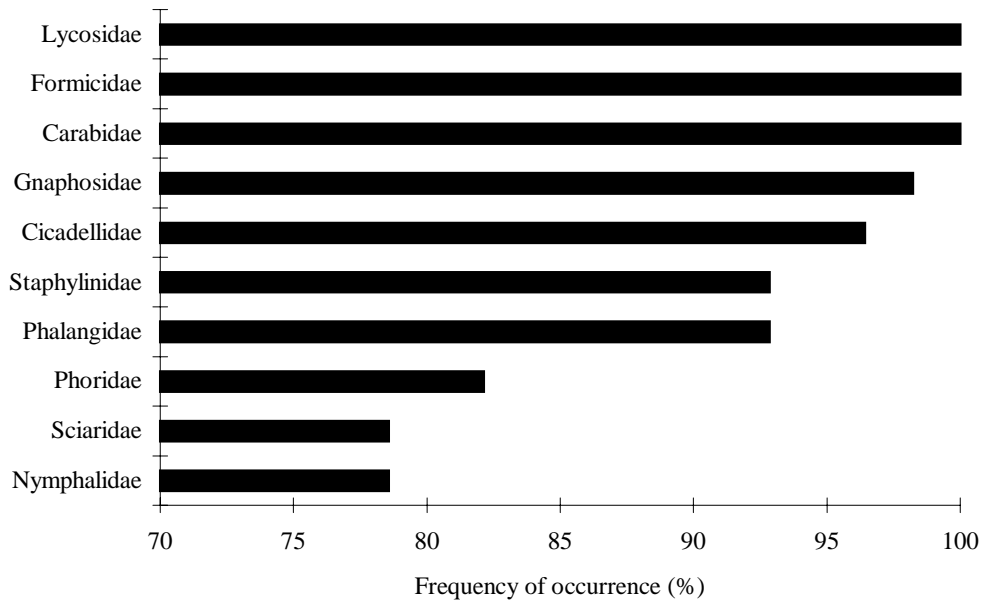
FIG. 43. Ten most frequently occurring invertebrate families. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin.

Regression Model for Invertebrate Richness

    Regression on abiotic environmental variables resulted in a 2-variable model: a positive association with precipitation and a negative association with west aspects (adj. $R^2 = 0.140$) (Table 105). Regression on channel characteristics resulted in a one-variable model: a negative association with gradient (adj. $R^2 = 0.211$). Regression on vegetation characteristics resulted in a 3-variable model: positive associations with alder−willow, meadow, and lodgepole pine (adj. $R^2 = 0.358$). The final backwards regression on these 4 key variables resulted in a robust 3-variable model showing that invertebrate richness increased with increases in alder−willow and meadow, and decreases in channel gradient (adj. $R^2 = 0.404$) (Tables 105 and 106).

TABLE 104. Significant correlations ($P \leq 0.10$) between invertebrate family richness and 22 environmental variables. Bolded values indicate $P \leq 0.05$. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

	Invertebrate family richness	
Environmental variable	r	*P*
Channel characteristics:		
Gradient	**-0.475**	**<0.001**
Sinuosity	0.233	0.085
Vegetation characteristics:		
Mixed conifer	**-0.400**	**0.002**
Lodgepole pine	**0.307**	**0.021**
Alder−willow	**0.433**	**0.001**
Meadow	**0.409**	**0.002**
Large log	**-0.309**	**0.021**

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TABLE 105. Variables selected in step-wise regressions for invertebrate family richness and 3 groups of environmental variables ($n = 22$). N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

Environmental variable	Invertebrate family richness
Channel characteristics:	
Gradient	**N**
Vegetation characteristics:	
Lodgepole pine	P
Alder−willow	**P**
Meadow	**P**
Variables in final model	*3*
adj. R^2	*0.404*

TABLE 106. Final backwards regression model for invertebrate family richness relative to environmental variables. Data were collected at sample reaches ($n = 56$) in the Lake Tahoe basin in 1996. Beta = partial regression coefficient.

Environmental variables	B	SE of B	Beta	T	P
Alder−willow	25.32	6.85	0.391	3.695	<0.001
Meadow	13.00	4.79	0.305	2.715	0.009
Channel gradient	-4.86	1.85	-0.300	-2.635	0.011

I looked for potential thresholds in family richness in relation to the 3 environmental variables selected in the final regression model. A threshold was shown with meadow, where at least 50 invertebrate families were present where meadow occupied $\geq 30\%$ of the reach (Fig. 44). Invertebrate family richness was significantly greater on reaches with $\geq 30\%$ meadow (1-tailed test, pooled variance, $t = 3.34$, $P = 0.010$).

Invertebrate Richness by Environmental Gradients
    Invertebrate family richness showed few correlations with the 7 environmental gradients defined by PCA (see Environmental Characteristics section above) (Table 107). Significant positive correlations were observed between invertebrate family richness and the channel flow, forest to meadow, and alder−willow gradients. Invertebrate family richness was significantly negatively correlated with the snag and log gradient.

Invertebrate Richness by Basin Orientation
    The number of reaches sampled in 1996 in each orientation were relatively equivalent (north = 14, east = 14, south = 13, west = 15). Family richness did not vary by basin orientation (ANOVA, $P = 0.165$).
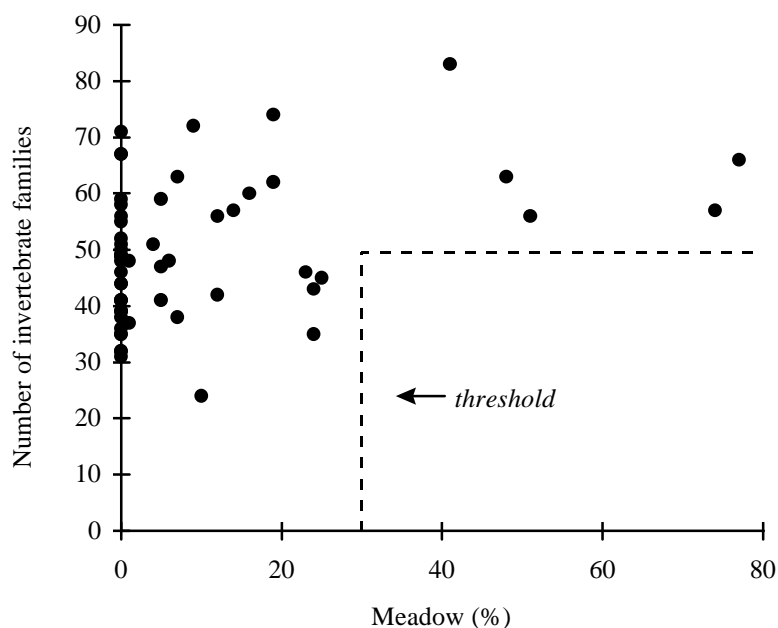
FIG. 44. Threshold between meadow and the richness of invertebrate families. Data were collected on 56 sample reaches in the Lake Tahoe basin in 1996.

TABLE 107. Significant ($P \leq 0.10$) correlations between environmental gradients (as defined by principal components analysis) and invertebrate family richness and Lepidoptera genus richness. Bolded values indicate $P \leq 0.05$. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

Environmental gradient	Invertebrate family richness		Lepidoptera genus richness	
	r	*P*	r	*P*
Physical gradient:				
1. Elevation−precipitation	-0.127	0.352	0.024	0.863
2. Channel flow	**0.355**	**0.007**	0.139	0.306
Vegetation gradient:				
1. Forest to meadow	**0.474**	**<0.001**	0.125	0.361
2. Subalpine vegetation	0.009	0.947	0.041	0.765
3. Alder−willow	**0.388**	**0.003**	-0.035	0.797
4. Aspen−cottonwood	0.204	0.131	-0.096	0.481
Woody debris gradient:				
1. Snag and log	**-0.256**	**0.057**	0.195	0.149

Patterns of Lepidoptera Diversity

General Patterns

Lepidoptera diversity was described by taxonomic richness and genera richness. These 2 variables were highly correlated (r = 0.851, $P < 0.001$), and so genera richness was used to represent lepidoptera diversity because it facilitates the identification and discussion of specific taxa. A total of 15 genera were observed on sample reaches (Table 108), of which 80% ($n = 12$) were present on less than 25% of the sample reaches. The 3 genera present on over 25% of the reaches were Anthocharis (Orange-tip) ($n = 17$ observations), Papilio (swallowtail) ($n = 18$ observations), and Clossinna (meadow fritillary) ($n = 41$ observations), and they accounted for approximately 73% of all observations. Leptidoptera richness varied from 0 to 6 genera per reach ($\bar{x} = 1.7$, SE = 0.15).

Environmental Relationships of Lepidoptera Richness

Regression Model for Lepidoptera Richness

Lepidoptera richness was correlated with only one of the 22 environmental variables: a negative correlation with north aspects (r = -0.225, $P = 0.045$). Channel and vegetation variable analyses resulted in no variables being selected. Regression on abiotic environmental variables resulted in a weak one-variable model, where lepidoptera richness decreased in association with north aspects (adj. R^2 = 0.038, B = -0.714, SE of B = 0.350, Beta = -0.225, T = -2.038, $P = 0.045$).

TABLE 108. Lepidoptera genera detected and their frequency of occurrence. Data were collected on 56 sample reaches in the Lake Tahoe basin in 1996.

Lepidoptera genus	Frequency of occurrence	Percent of reaches occupied
Classiana	41	73.2
Papilio	18	32.1
Anthoarous	17	30.3
Basilarchia	9	16.0
Adelpha	6	10.7
Hesperia	4	7.1
Aglais	1	1.8
Celastrina	1	1.8
Neophasia	1	1.8
Nymphalis	1	1.8
Occidryas	1	1.8
Parnassius	1	1.8
Polygonia	1	1.8
Satyrium	1	1.8
Thorybes	1	1.8

Lepidoptera Richness by Environmental Gradients and Basin Orientation

No significant correlations were observed between Lepidopera richness and any of the 8 environmental gradients (Table 108). Similarly, Lepidoptera richness did not vary by basin orientation (ANOVA, $P = 0.447$).

Patterns of Invertebrate Alpha Diversity by Habitat Association

General Patterns

Patterns of invertebrate richness were explored in relation to association with 3 life history traits based on habitat associations: aquatic, semi-aquatic, and terrestrial. Approximately 14% ($n = 28$) of all families were identified as aquatic, 5% ($n = 11$) were semi-aquatic, and the remaining 81% ($n = 164$) were terrestrial (Table 109). The average number of aquatic and semi-aquatic families per reach were similar, where at the average number of terrestrial families per reach was over 10 times greater than the average number of aquatic and semi-aquatic families (Table 109). At least one aquatic and semi-aquatic family occurred on most reaches, with their frequency of occurrence being 95% and 98%, respectively. Aquatic family richness was not correlated with either semi-aquatic family richness ($r = 0.109$, $P = 0.424$) or terrestrial family richness ($r = 0.020$, $P = 0.884$), however, semi-aquatic family richness was correlated with terrestrial family richness ($r = 0.341$, $P = 0.010$).

TABLE 109. Descriptive statistics for the richness of 3 family groups based on habitat associations. Data were collected at sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

Habitat group	Total families possible	Minimum	Maximum	Average	SE
Aquatic	28	0	7	2.80	0.22
Semi-aquatic	11	0	7	3.14	0.21
Terrestrial	164	24	80	43.87	1.47

The contribution of individual families to the richness values for each group varied based on the relative frequency of the families. The majority (84%) of the 25 aquatic families occurred on > 1 sample reach. Eleven aquatic families were present on ≥ 5 sample reaches (Fig. 45) and they accounted for 79% of all detections of aquatic families. These 11 families consisted of 5 stoneflies (Plecoptera), 1 caddisfly (Trichoptera), 1 mayfly (Ephemeroptera), 1 damselfly (Odonata), 1 mollusc (Veneroida), and 2 true bugs (Hemiptera). The remaining 14 families consisted of additional mayfly ($n = 3$), caddisfly ($n = 3$), true bug ($n = 1$), beetle (Coleptera, $n = 3$), fly (Diptera, $n = 2$), and mollusc ($n = 2$) families. Gerridae and Nemouridae were the most frequently occurring aquatic families, and they occurred on almost twice as many reaches as the next most frequent aquatic family, Chloroperlidae.

Of the 11 semi-aquatic families, Simuliidae and Culicidae were the most frequently occurring families, occurring 30% more frequently than the next most frequent family, Tabanidae. Eight of the 11 semi-aquatic families were flies (Diptera) (Fig. 46). The remaining 3 families were springtail (Collembola), true bug, and beetle families (Fig. 46).
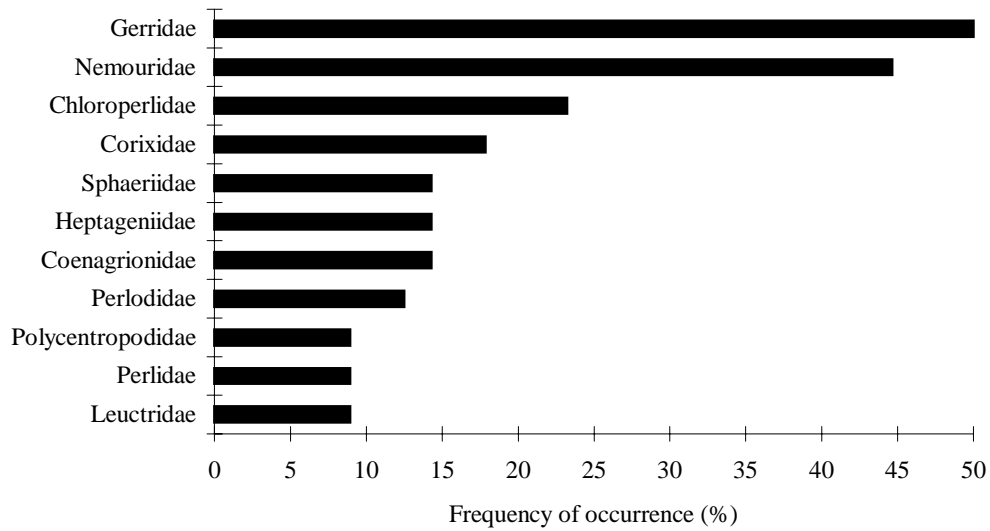
FIG. 45. Aquatic invertebrate families occurring on ≥ 5 sample reaches. Data were collected on 56 sample reaches in the Lake Tahoe basin in 1996.

The 10 most frequent terrestrial families were also the 10 most frequent of all families (Fig. 43). The 10 most frequent terrestrial families ranged from 78 to 100% frequency of occurrence and accounted for 21% of all observations of terrestrial families.
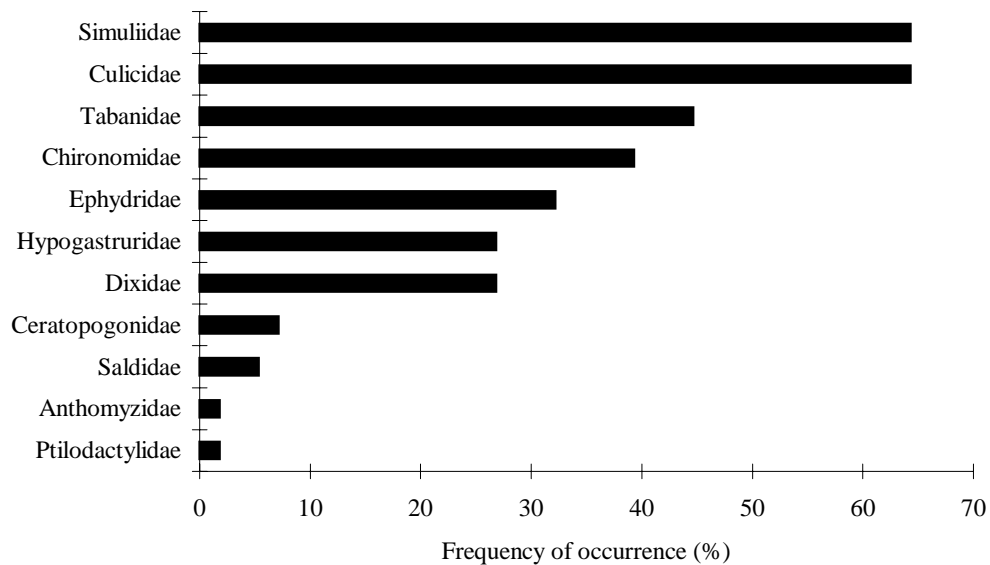

FIG. 46. Semi-aquatic invertebrate families. Data were collected on 56 sample reaches in the Lake Tahoe basin in 1996.

Environmental Relationships of Invertebrate Groups
Correlations

     Aquatic and terrestrial family richness were each correlated with many different environmental variables, whereas the richness of semi-aquatic families was correlated with only one environmental variable (alder–willow) (Table 110). No variables shifted from negative to positive correlations between aquatic and terrestrial families, however alder–willow appeared to have a decreasing association with richness from terrestrial to aquatic families. Channel gradient was the one variable that was similarly correlated (negatively) with both aquatic and terrestrial family richness. Aquatic family richness was uniquely correlated positively with precipitation, channel width, and channel log volume, and negatively with west aspect, canopy cover index, and elevation. These correlations indicate a strong relationship between the richness of aquatic families and physical features of the environment. Conversely, the richness of terrestrial families appeared to be more strongly influenced by the composition and structure of vegetation, including positive correlations with alder–willow, meadow, and lodgepole pine, and a negative correlation with mixed conifer, large logs, and large and small snags.

Regression Model for Aquatic Invertebrate Richness

     Regression of aquatic invertebrate family richness on abiotic environmental variables resulted in a 3-variable model: positive associations with precipitation and north aspects, and a negative association with elevation (adj. $R^2 = 0.220$) (Table 111). Regression on channel variables resulted in a one-variable model: a positive association with channel width (adj. $R^2 = 0.152$). Regression on vegetation variables resulted in a one variable model: a negative association with canopy cover index (adj. $R^2 = 0.050$). Backwards step-wise regression on these 5 key variables resulted in the 3-variable abiotic environment model, where aquatic invertebrate richness increased with increases in precipitation and in association with north aspects, and with decreases in elevation (adj. $R^2 = 0.220$) (Tables 111 and 112).

TABLE 110. Significant correlations ($P \leq 0.10$) between family richness for 3 invertebrate groups and 22 environmental variables. Bolded values indicate $P \leq 0.05$. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

| | Invertebrate habitat group | | | | | |
| | Aquatic families | | Semi-aquatic families | | Terrestrial families | |
Environmental variable	r	*P*	r	*P*	r	*P*
Abiotic environment:						
Elevation	-0.232	0.086	N	n.s.	N	n.s.
Precipitation	**0.285**	**0.033**	P	n.s.	P	n.s.
West	**-0.280**	**0.037**	N	n.s.	N	n.s.
Channel characteristics:						
Gradient	**-0.324**	**0.015**	N	n.s.	**-0.441**	**0.001**
Width	**0.409**	**0.022**	N	n.s.	P	n.s.
Sinuosity	P	n.s.	P	n.s.	0.228	0.090
Vegetation characteristics:						
Mixed conifer	N	n.s.	N	n.s.	**-0.402**	**0.002**
Alder−willow	P	n.s.	**0.329**	**0.013**	**0.410**	**0.022**
Meadow	P	n.s.	P	n.s.	**0.436**	**0.001**
Canopy cover index	**-0.260**	**0.053**	P	n.s.	N	n.s.
Lodgepole pine	P	n.s.	P	n.s.	**0.311**	**0.020**
Large log	N	n.s.	N	n.s.	**-0.322**	**0.015**
Small snag	N	n.s.	P	n.s.	-0.237	0.079
Large snag	N	n.s.	P	n.s.	-0.239	0.076
Channel log volume	0.230	0.088	N	n.s.	P	n.s.

TABLE 111. Variables selected in step-wise regressions between 3 groups of environmental variables ($n = 22$) and family richness for 3 invertebrate groups. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

Environmental variable	Invertebrate habitat group		
	Aquatic families	Semi-aquatic families	Terrestrial families
Abiotic environment:			
Elevation	**N**	-	-
Precipitation	**P**	-	-
North aspect	**P**	-	-
Channel characteristics:			
Gradient	-	-	**N**
Width	P	-	-
Vegetation characteristics:			
Alder−willow	-	**P**	**P**
Meadow	-	-	**P**
Canopy cover index	N	-	-
Variables in final model	*3*	*1*	*3*
adj. R^2	*0.220*	*0.093*	*0.384*

TABLE 112. Final linear regression model of environmental variables in relation to family richness of 3 habitat groups (aquatic, semi-aquatic, and terrestrial). Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	P
Aquatic family richness:					
Elevation	-9.394	2.780	-0.444	-3.380	0.001
Precipitation	2.007	0.616	0.416	3.257	0.002
North aspect	0.938	0.484	0.239	1.937	0.058
Semi-aquatic family richness:					
Alder−willow	2.873	1.121	0.329	2.562	0.013
Terrestrial family richness:					
Alder−willow	22.590	6.392	0.380	3.534	<0.001
Meadow	13.447	4.467	0.344	3.010	0.004
Channel gradient	-3.764	1.721	-0.253	-2.187	0.033

Meso-scale disturbance (measured as the proportion of the area within 250 m of the center of the reach that is physically disturbed) was negatively correlated with elevation ($r = -0.515$, $P < 0.001$) and precipitation ($r = -0.358$, $P = 0.007$) in the basin. It is possible that the relationships observed between aquatic family richness and elevation and precipitation were an indirect

reflection of disturbance. An analysis of covariance with elevation partitioned into 4 equal sized segments, and meso-scale disturbance as the covariate showed that aquatic family richness did not vary significantly among elevation segments when the influence of disturbance was removed, however aquatic family richness did not vary significantly by disturbance either (Table 113). The same analysis conducted in relation to precipitation showed that aquatic family richness was no longer statistically significant, and that disturbance was not associated with aquatic family richness.

I looked for a potential thresholds between aquatic family richness and the 3 variables selected in the final environmental model. I found that ≥ 2 aquatic families were always present on reaches where precipitation exceeded 110 cm/yr (Fig. 47). Aquatic family richness was significantly greater on reaches where precipitation exceeded 110 cm/yr (1-tailed test, pooled variance, $t = 2.16$, $P = 0.022$).

TABLE 113. Analysis of covariance exploring the relationship between aquatic family richness and elevation and precipitation with disturbance as a covariate. SS = sum of squares. ν = degrees of freedom. MS = mean square.

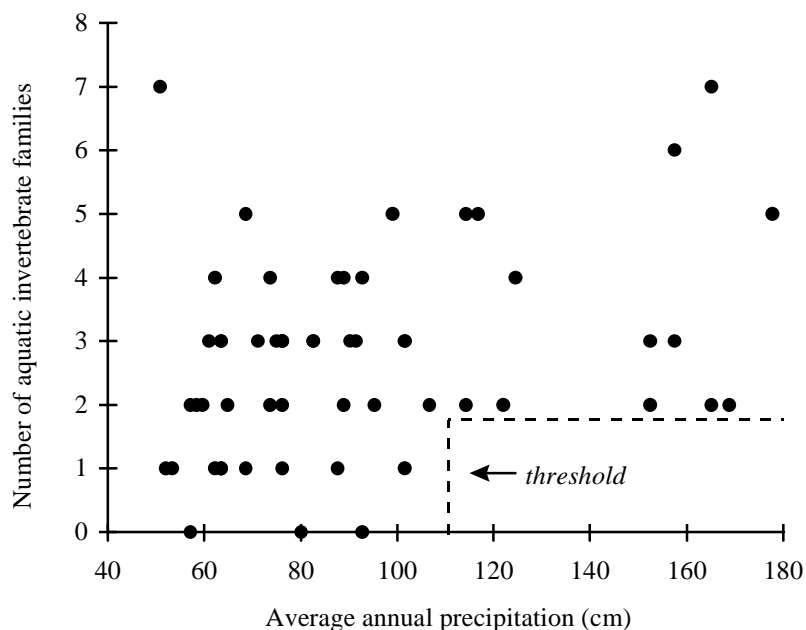| Source of variation	SS	ν	MS	F	*P*
Elevation:					
Within + residual	134.55	51	2.64		
Regression	1.35	1	1.35	0.51	0.478
Elevation	10.11	3	3.37	1.28	0.292
Model	10.29	4	2.57	0.97	0.429
Total	144.84	55	2.63		
Precipitation:					
Within + residual	129.18	51	2.53		
Regression	3.17	1	3.17	1.25	0.268
Precipitation	15.48	3	5.16	2.04	0.120
Model	15.65	4	3.91	1.55	0.203
Total	144.84	55	2.63		

Fig. 47. Threshold between precipitation and the richness of aquatic invertebrate families. Data were collected on 56 sample reaches in the Lake Tahoe basin in 1996.

Regression Model for Semi-aquatic Invertebrate Richness

Regression of semi-aquatic family richness on abiotic environmental variables and channel variables resulted in no variables being selected (Table 111). Regression on vegetation variables resulted in a weak one-variable model, where semi-aquatic family richness increased with increases in alder–willow (adj. $R^2 = 0.092$) (Tables 111 and 112). No threshold was observed between semi-aquatic family richness and alder–willow abundance.

Regression Model for Terrestrial Invertebrate Richness

Regression of terrestrial family richness on abiotic environmental variables resulted in no variables being selected (Table 111). Regression on channel variables resulted in a one-variable model: a negative association with channel gradient (adj. $R^2 = 0.080$). Regression on vegetation variables resulted in a 2-variable model: positive associations with alder–willow and meadow (adj. $R^2 = 0.400$). Backwards step-wise regression on these 3 key variables resulted a 3-variable model, where invertebrate richness increased with increases in alder–willow and meadow and decreases in channel gradient (adj. $R^2 = 0.384$) (Tables 111 and 112).

I looked for potential thresholds in terrestrial family richness in relation to the 3 variables selected in the final regression model. It appeared that once the area occupied by meadow exceeded 30%, terrestrial family richness did not fall below 50 families (Fig. 48). Terrestrial family richness was significantly greater where meadow exceeded 30% (1-tailed test, pooled variance, $t = 2.58$, $P = 0.031$).
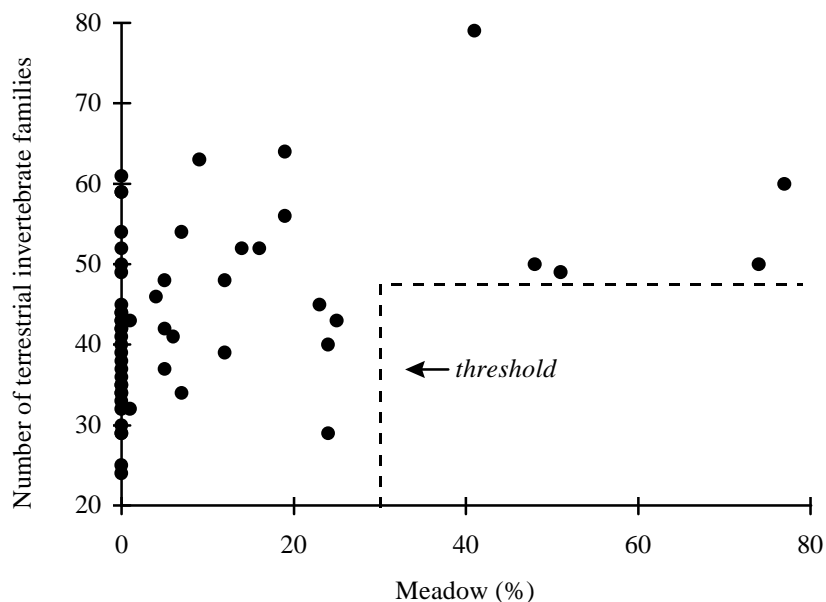
FIG. 48. Threshold relationship between meadow and the richness of terrestrial invertebrate families. Data were collected on 56 sample reaches in the Lake Tahoe basin in 1996.

Invertebrate Group Richness by Environmental Gradients

Invertebrate groups differed in their relationships with environmental gradients, closely reflecting their regression relationships with individual environmental variables (Table 114). Aquatic family richness was positively associated with channel flow, but did not exhibit a correlation with the elevation–precipitation gradient. The lack of correlation with this gradient is probably because aquatic family richness had opposing relationships with elevation and precipitation, whereas along this gradient they vary together. Semi-aquatic family richness was correlated with only the alder–willow gradient. Terrestrial family richness was correlated with the channel flow gradient and strongly correlated with forest to meadow and alder–willow gradients, reflecting the correlations observed with meadow, mixed conifer, and alder–willow in the analysis of individual environmental variables.

TABLE 114. Correlations between invertebrate group variables and principal component analysis factors. Bolded values indicate significant correlations ($P \leq 0.10$). r = correlation coefficients. Data were collected at sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

| | Invertebrate habitat groups | | | | | |
| | Aquatic family richness | | Semi-aquatic family richness | | Terrestrial family richness | |
Environmental gradient	r	*P*	r	*P*	r	*P*
Physical gradient:						
1. Elevation–precipitation	-0.047	0.729	0.043	0.752	-0.134	0.325
2. Channel flow	**0.447**	**<0.001**	0.087	0.523	**0.308**	**0.021**
Vegetation gradient:						
1. Forest to meadow	0.085	0.534	0.086	0.531	**0.488**	**<0.001**
2. Subalpine vegetation	0.003	0.983	-0.024	0.862	0.013	0.926
3. Alder–willow	0.059	0.667	**0.322**	**0.016**	**0.367**	**0.005**
4. Aspen–cottonwood	0.057	0.676	0.046	0.739	0.206	0.128
Woody debris gradient:						
1. Snag and log	0.055	0.685	0.061	0.654	-0.179	0.186

Invertebrate Group Richness by Basin Orientation

The richness of aquatic families varied significantly by basin orientation ($\nu = 3, 52$; SS = 21.12, 119.38; MS = 7.04, 2.30; F = 3.07, $P = 0.036$). Richness was higher on the south and west sides (where precipitation is higher) compared to the north and east sides of the basin, with the south side having significantly greater richness than the east side (re: Tukey's test). The richness of semi-aquatic and terrestrial families did not differ by basin orientation ($P = 0.197$ and 0.206, respectively).

Patterns of Invertebrate Rarity

General Patterns

Over 60% of all families ($n = 124$) had a frequency of occurrence of less than 25% ($n < 14$ reaches), whereas only 10 families occurred on more than 75% of the reaches (Fig. 49). Approximately 52% of the invertebrate families (106 of 203) were present on less than 10% of the reaches, and they were considered rare. The average number of rare families per reach was 4.7 compared to an average of 45.2 common families per reach (Table 115). Rare families were observed on all but one of the reaches. Similarly, the percent of all families that were rare at each reach averaged less than 10%, whereas common families averaged over 90%.
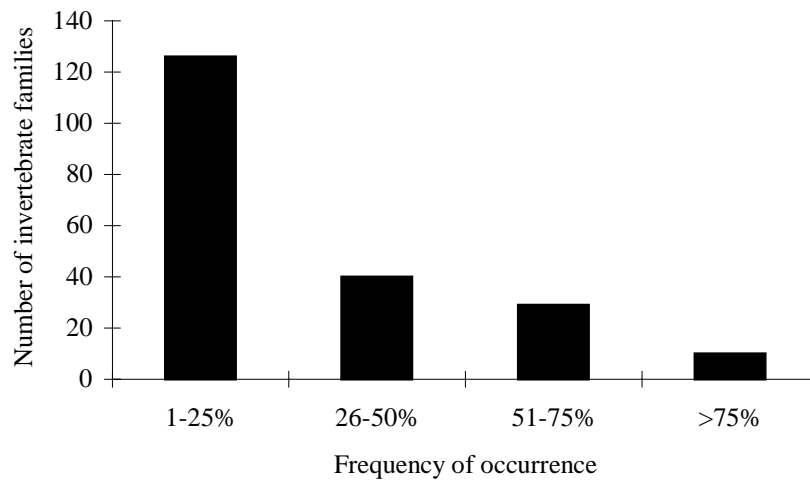
FIG. 49. Number of invertebrate families occurring in each of 4 frequency of occurrence intervals. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

TABLE 115. Descriptive statistics for measures of frequency class variables for invertebrate family occurrence. Families considered rare if frequency of occurrence < 10%, common if $\geq$ 10%. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

Frequency class variable	Minimum	Maximum	Average	SE
Number of rare families	0	14	4.68	0.36
Number of common families	27	69	45.18	1.38
Percent rare families	0	18.6	9.2	0.58
Percent common families	81.4	100.0	90.8	0.58

Significant correlations were observed among the 4 measures of frequency (Table 116). The high correlations between number of rare families and the percent of both rare and common families, indicated that the most informative patterns of association could be discerned by analyzing the number of rare versus common families.

TABLE 116. Significant ($P \leq 0.10$) correlations among invertebrate frequency class variables. Bolded values indicate $P \leq 0.05$. Shading indicates redundant cells. Data were collected at sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

Frequency class variable	Number of rare families		Number of common families		Percent rare families	
	r	P	r	P	r	P
Number of rare families						
Number of common families	**0.774**	**<0.001**				
Percent rare families	**0.854**	**<0.001**	0.020	0.885		
Percent common families	**-0.854**	**<0.001**	-0.020	0.885	**1.000**	**<0.001**

Environmental Relationships of Invertebrate Rarity
Correlations
    The richness of both rare and common families was positively correlated with alder−willow and meadow (Table 117). The richness of both rare and common families was also negatively correlated with gradient, mixed conifer, and large logs. The richness of rare families was also uniquely negatively associated with large and small snags, and positively correlated with shrubs. The richness of common families was uniquely positively correlated with lodgepole pine and sinuosity.

TABLE 117. Significant ($P \leq 0.10$) correlations between invertebrate family frequency class variables and 22 environmental variables. Bolded values indicate $P \leq 0.05$. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

| | Invertebrate frequency classes | | | |
| | Number of rare families | | Number of common families | |
Environmental variables	r	*P*	r	*P*
Channel characteristics:				
Gradient	**-0.329**	**0.013**	**-0.461**	**<0.001**
Sinuosity	N	n.s.	**0.282**	**0.036**
Vegetation characteristics:				
Mixed conifer	-0.220	0.100	**-0.403**	**0.002**
Lodgepole pine	P	n.s.	**0.328**	**0.014**
Alder−willow	0.254	0.059	**0.432**	**0.001**
Shrub	0.253	0.059	N	n.s.
Meadow	**0.439**	**0.001**	**0.356**	**0.007**
Large snag	**-0.353**	**0.008**	N	n.s.
Small snag	**-0.293**	**0.029**	N	n.s.
Large log	**-0.373**	**0.005**	-0.257	0.055

Regression Model for Rare Invertebrate Richness
    The number of rare families was compared to environmental variables using multiple regression (Table 118). Regression on abiotic environmental variables resulted in no variables being selected. Regression on channel characteristics resulted in a 2-variable model: negative associations with gradient and width (adj. $R^2 = 0.131$). Regression on vegetation characteristics resulted in a 2-variable model: positive associations with alder−willow and meadow (adj. $R^2 = 0.233$). Backwards regression on these 4 key variables resulted in the 2-variable vegetation model, where the richness of rare invertebrate families increased with increases in alder−willow and meadow (adj. $R^2 = 0.233$) (Tables 118 and 119).

TABLE 118. Variables selected in step-wise regressions between 3 groups of environmental variables ($n = 22$) and the number of families in each of 2 invertebrate frequency classes in the Lake Tahoe basin. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected at 56 sample reaches in 1996.

| | Invertebrate frequency class | |
| | Number of | Number of |
Environmental variable	rare families	common families
Channel character:		
Gradient	N	**N**
Width	N	-
Vegetation character:		
Alder−willow	**P**	P
Meadow	**P**	**P**
Lodgepole pine	**-**	P
Variables in final model	*2*	*3*
adj. R^2	*0.233*	*0.408*

TABLE 119. Final backwards regression model of key environmental variables related to invertebrate frequency class variables. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Number of rare invertebrate families:					
Meadow	4.32	1.15	0.444	3.756	<0.001
Alder−willow	3.89	1.75	0.262	2.223	0.031
Number of common invertebrate families:					
Alder−willow	21.79	6.13	0.388	3.552	<0.001
Gradient	-4.31	1.65	-0.307	-2.611	0.012
Meadow	9.22	4.29	0.250	2.150	0.036

Regression Model for Common Invertebrate Richness

The number of common families was compared to environmental variables using multiple regression (Table 118). Regression on abiotic environmental variables resulted in no variables being selected. Regression on channel characteristics resulted in a one-variable model: a negative association with gradient (adj. $R^2 = 0.198$). Regression on vegetation variables resulted in a 3-variable model: positive relationships with alder−willow, lodgepole pine, and meadow (adj. $R^2 = 0.327$). Backward regression on these 4 key variables resulted in a 3-variable model, where the richness of common invertebrate families increased with increases in alder−willow and meadow, and decreases in channel gradient (adj. $R^2 = 0.408$) (Tables 118 and 119).

Invertebrate Rarity by Environmental Gradients

In general, rare and common family richness had dissimilar relationships with environmental gradients (Table 120). The number of both rare and common invertebrate families was positively correlated with the forest to meadow gradient. The remaining relationships differed between the two variables. The number of rare families was positively correlated with the aspen−cottonwood gradient and negatively correlated with the snag and log gradient. The number of common families was positively correlated with the alder−willow and channel flow gradients.

TABLE 120. Significant ($P \leq 0.10$) correlations between invertebrate frequency class variables and environmental gradients (as defined by principal components analysis). Bolded values indicate $P \leq 0.05$. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

Environmental gradient	No. rare families		No. common families	
	r	*P*	r	*P*
Physical gradient:				
1. Elevation−precipitation	-0.219	0.105	-0.088	0.517
2. Channel flow	0.098	0.472	**0.383**	**0.004**
Vegetation gradient:				
1. Forest to meadow	**0.338**	**0.001**	**0.458**	**<0.001**
2. Subalpine vegetation	0.067	0.622	-0.007	0.957
3. Alder−willow	0.169	0.214	**0.404**	**0.002**
4. Aspen−cottonwood	**0.348**	**0.009**	0.144	0.290
Woody debris gradient:				
1. Snag and log	**-0.359**	**0.007**	-0.204	0.132

Invertebrate Rarity by Basin Orientation

The richness of rare invertebrate families did not vary among basin orientations (ANOVA, $P = 0.771$). The richness of common families did differ among orientations ($\nu = 3, 52$; SS = 658.70, 5167.52; MS = 291.57, 99.38; F = 2.210, $P = 0.098$). Common family richness was greatest on the west side, followed by the south, east, and then north sides of the basin, although no pair-wise comparisons were significantly different (re: Tukey's test).

Patterns of Invertebrate Beta Diversity

Invertebrate Turnover along Environmental Gradients
Family Turnover

The lower of the gains and losses between the lower and upper segments ("total turnover") was used as the primary indication of the contribution of a gradient to beta diversity (Table 121). The alder−willow gradient had the highest family turnover ($n = 83$ families), constituting over 30% of all families encountered. The remaining 8 gradients showed progressively lower turnover, being lower by 2-3 families with each gradient. The gradient with the second highest turnover was channel flow ($n = 80$ families), followed by subalpine vegetation ($n = 79$ families), aspen−cottonwood ($n = 76$ families), precipitation ($n = 73$ families), and elevation ($n = 71$ families).

TABLE 121. Beta diversity index values for invertebrate families within and among 9 environmental gradients. The number of families per segment, the number of families only occurring at upper ("gains") or lower ("losses") ends of the gradient, and Whittaker's beta diversity index (β_w) are displayed. A modified version of Whittaker's beta diversity index (β_{wMIN}) is also displayed. Bolded values indicate turnover. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

Gradient	Richness of lower segment	Richness of higher segment	Total richness	Gains	Losses	$\beta_w{}^*$	β_{wMIN}†
Elevation:							
seg1:seg2	153	145	179	**26**	34	0.204	0.169
seg2:seg3	145	140	172	**27**	32	0.210	0.193
seg3:seg4	140	140	158	**18**	18	0.132	0.128
average							*0.163*
low:high	*179*	*172*	*203*	*24*	*31*	*0.209*	*0.139*
Precipitation:							
seg1:seg2	150	144	177	**27**	33	0.207	0.179
seg2:seg3	144	142	171	**27**	29	0.199	0.194
seg3:seg4	142	140	166	**24**	26	0.180	0.168
average							*0.180*
low:high	*177*	*166*	*203*	*26*	*37*	*0.188*	*0.152*
Elevation–precipitation:							
seg1:seg2	153	140	177	**24**	37	0.214	0.162
seg2:seg3	140	150	173	33	**23**	0.196	0.169
seg3:seg4	150	131	167	**17**	36	0.189	0.113
average							*0.148*
low:high	*177*	*167*	*203*	*26*	*36*	*0.185*	*0.145*
Channel flow:							
seg1:seg2	140	142	166	26	**24**	0.180	0.168
seg2:seg3	142	142	171	29	**29**	0.210	0.210
seg3:seg4	142	149	174	32	**25**	0.199	0.175
average							*0.184*
low:high	*166*	*174*	*203*	*37*	*29*	*0.199*	*0.171*
Forest to meadow:							
seg1:seg2	125	143	159	34	**16**	0.187	0.112
seg2:seg3	143	140	161	**18**	21	0.138	0.126
seg3:seg4	140	162	184	46	**22**	0.224	0.134
average							*0.124*
low:high	*159*	*184*	*203*	*44*	*19*	*0.188*	*0.102*

TABLE 121 cont.

Gradient	Richness of lower segment	Richness of higher segment	Total richness	Gains	Losses	β_w*	β_{wMIN}†
Subalpine vegetation:							
seg1:seg2	148	138	173	**25**	35	0.213	0.168
seg2:seg3	138	144	167	29	**23**	0.184	0.160
seg3:seg4	144	143	174	**30**	31	0.215	0.215
average							*0.181*
low:high	*173*	*174*	*203*	*30*	*29*	*0.175*	*0.171*
Alder–willow:							
seg1:seg2	136	144	169	33	**25**	0.210	0.172
seg2:seg3	144	147	174	30	**27**	0.201	0.189
seg3:seg4	147	148	177	30	**29**	0.203	0.203
average							*0.188*
low:high	*169*	*177*	*203*	*34*	*26*	*0.178*	*0.152*
Aspen–cottonwood:							
seg1:seg2	136	144	167	31	**23**	0.196	0.159
seg2:seg3	145	139	170	**25**	31	0.204	0.179
seg3:seg4	139	154	181	42	**27**	0.238	0.174
average							*0.171*
low:high	*167*	*181*	*203*	*36*	*22*	*0.171*	*0.126*
Snag and log:							
seg1:seg2	157	133	177	**20**	44	0.223	0.127
seg2:seg3	133	140	159	26	**19**	0.165	0.136
seg3:seg4	140	139	164	24	**25**	0.179	0.179
average							*0.147*
low:high	*177*	*164*	*203*	*26*	*39*	*0.195*	*0.152*

* Whittaker's beta diversity index: S/α - 1, where S = total family richness, and α = the average family richness of the two segments being compared.

† Modified Whittaker's beta diversity index: (S/s-max) - 1, where S = total family richness, and s-max = the highest richness of the two segments being compared, resulting in a minimum beta diversity index value.

Patterns of turnover along each gradient provide additional insights as to their contributions to beta diversity based on presence (Table 121). Along the elevation gradient, total richness declined substantially from the low to the high end of the gradient, and turnover was highest mid gradient and lowest at the upper most elevations. Total richness declined, as did turnover, along the precipitation gradient from low to high precipitation. Patterns in total richness and turnover along the elevation–precipitation gradient were almost identical to those observed along the precipitation gradient. Along the channel flow gradient, total richness increased, whereas turnover was highest at mid gradient. Total richness increased along the forest to meadow gradient, and both richness and turnover were substantially higher in association with the upper most segments of the gradient, which represented meadow. Along the subalpine vegetation gradient, total richness was lowest mid gradient, and turnover was highest at the upper end of the gradient. Total richness and turnover both increased along the alder–willow gradient and the aspen–cottonwood gradients. Finally, total richness decreased while turnover increased along the snag and log gradient, an unusual pattern relative to the other gradients

Whittaker's Index of Beta Diversity

The gradients were evaluated for their relative contribution to beta diversity in part based on a modified Whittaker's beta diversity index (β_{wMIN}), with the unmodified index value provided for comparison (Table 121). The average β_{wMIN} for segment comparisons along each gradient varied from a low of 0.124 for the forest to meadow gradient, to a high of 0.188 for the alder−willow gradient. Next to alder−willow, the channel flow, subalpine vegetation, and aspen−cottonwood gradients had the next highest average β_{wMIN} values (0.184, 0.181, and 0.171, respectively). The remaining gradients had much lower average β_{wMIN} values.

Family Presence

Family presence contributions to beta diversity are displayed in Tables 122 to 124. Families contributing to gains and losses between lower and upper segments of each gradient are indicated, along with families showing additional trends of presence (absent from segment 1 or 4) along the gradient. Family specific associations with gradients also indicate the relevance of the gradient to individual families. A total of 68 families (33.2%) were present on more than one reach and absent from one or the other end of one or more gradients. Of these 68 families, 17 were absent along portions of only one gradient (Tables 122 to 124). Families with a frequency of occurrence ≥ 10% or only absent along one gradient are likely to be the most affected by associated gradients. Approximately 25% of the gains and losses accounted in Table 121 can be attributed to families occurring on more than one reach.

Along the elevation gradient, 6 families were restricted to higher elevation reaches, with 4 additional families absent from the lowest elevation reaches (Table 122). One of the 4 families absent from lowest elevation reaches, Pompilidae, was present on over 10% of the reaches. Over twice as many families were restricted to lower elevation reaches (n = 15), with 3 additional families absent from the highest elevation reaches. Among these 3 families were the Largidae and Geometridae (inchworm) families which occur on ≥ 10% of the reaches. Along the precipitation gradient, 9 families were restricted to the lower end of the gradient, with an additional 7 families absent from the highest precipitation reaches. The Cercopidae (spittlebugs and froghoppers) and Hesperiidae (common skippers) families were among these 7 families, and were absent only along the precipitation gradient. The Hesperiidae was additionally present on ≥10% of the reaches. Only 6 families were restricted to upper precipitation reaches, with one additional family being absent from the lowest precipitation reaches. Along the elevation−precipitation gradient, a greater number (n = 9) of families were restricted to the lower end of the gradient, with 8 additional families absent from the upper most segments of the gradient. Among these 8 families were 3 that had frequencies ≥ 10%, Largidae (largid bugs), Anthophoridae (cuckoo bees, digger bees, and carpenter bees), and Delphacidae (Delphacid planthoppers), with Anthophoridae having a frequency > 10% and Delphacidae being absent along only the elevation−precipitation gradient. Three families were restricted to the upper end of the elevation− precipitation gradient, including Hemerobiidae (brown lacewings), which was present on >10% of the reaches. An additional 5 families were absent from the lowest elevation−precipitation reaches, including Anthophoridae which was present on >10% of the reaches and Andrenidae (Andrenid bees) which was only absent along this gradient. A comparable number of families were associated with each end of the channel flow gradient. Nine families were restricted to each of the lower and upper end of the gradient, with 4 and 5 families absent from the upper most and lower most segments, respectively. Three families present on ≥ 10% of the reaches were absent from the lower most reaches along the channel flow gradient: Largidae (largid bugs), Silphidae (carrion beetles), and Lonchopteridae (spear-winged flies).

TABLE 122. Families present on 2 or more reaches and absent from lower or upper segments of each of 2 abiotic environmental gradients. Gradients were defined by principal components analysis. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

Invertebrate family	Elevation low < ----- > high				Precipitation low < ----- > high				Elevation–precipitation gradient low < ----- > high				Channel flow gradient low < ----- > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Frequency < 10%:																
Arachnida -																
Hahniidae	X															X
Pholcidae	X				X				X_1				X			
Hexapoda -																
Antrodiaetidae												X				
Artematopidae	X															X
Bibionidae														X		
Cerambycidae			X							X						
Cercopidae[*]						X										
Colletidae			X													
Dermestidae			X					X								
Dytiscidae	X															X_4
Endomychidae	X_1				X				X							
Ephemerellidae													X			
Eriosomatidae		X						X			X				X	
Eupelmidae	X															
Heteroceridae	X															X
Hydropsychidae			X					X						X		
Leuctridae		X					X							X		
Lycidae					X				X				X			
Melittidae													X			
Membracidae	X							X_4								X_4
Melyridae	X															
Mymaridae									X				X			
Nitidulidae	X				X_1				X				X			

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TABLE 122 cont.

Invertebrate family	Elevation low < ------------------ > high				Precipitation low < ------------------ > high				Elevation–precipitation gradient low < -------------------- > high				Channel flow gradient low < ---------------------- > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Frequency < 10% cont:																
Pentatomidae	X															X_4
Perlidae						X				X						
Platygastridae	X															
Polycentropodidae		X				X				X						
Psychomyiidae				X				X_4				X_4				X
Psychodidae					X				X				X			
Ptilidae						X										
Reduviidae				X		X					X			X		
Rhyacophilidae													X_1			
Saldidae					X					X						
Chrysopidae												X				
Siphlonuridae	X									X						
Thripidae											X					
Thyreocoridae	X_1															X
Trixoscelididae	X				X				X_1							X
Xyelidae					X											
Mollusca -																
Euconulidae					X				X				X			
Pisiidae			X													
Zonitidae															X	

TABLE 122 cont.

Invertebrate family	Elevation low < ------------- > high				Precipitation low < ------------- > high				Elevation–precipitation gradient low < ------------- > high				Channel flow gradient low < ------------- > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Frequency ≥ 10%:																
Hexapoda -																
Andrenidae*											X					
Anthophoridae										X						
Delphacidae*										X						
Geometridae		X														
Hemerobiidae									X							
Hesperiidae						X										
Largidae		X								X						X
Lonchopteridae																X
Pompilidae			X													
Silphidae																X
Summary	15	3	4	6	9	7	1	6	9	8	5	3	9	4	5	9

* Only absent along one gradient.

[1] Only occurs on segment 1.

[4] Only occurs on segment 4.

TABLE 123. Families present on 2 or more reaches and absent from lower or upper segments of the snag and log gradient (derived by principal components analysis). Data were collected on sample reaches (n = 56) in the Lake Tahoe basin in 1996.

| | Snag and log gradient | | | |
| | low < ----------------------- > high | | | |
Invertebrate family	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Frequency < 10%:				
Arachnida -				
Pholcidae				X
Hexapoda -				
Antrodiaetidae	X_1			
Bibionidae	X			
Dermestidae				X
Dytiscidae				X
Ephemerellidae				X
Eriosomatidae				X_4
Heteroceridae				X
Lycidae	X			
Melyridae			X	
Pentatomidae	X_1			
Perlidae		X		
Saldidae		X		
Thripidae				X
Thyreocoridae	X_1			
Tiphiidae	X			
Trixoscelididae	X_1			
Xyelidae	X_1			
Mollusca -				
Pisiidae			X	
Zonitidae			X	
Frequency $\geq$ 10%:				
Hexapoda -				
Acroceridae		X		
Perlodidae[*]		X		
Chrysididae		X		
Silphidae		X		
Hemerobiidae			X	
Summary	8	6	4	7

[*] Only absent along one gradient.

[1] Only occurs on segment 1.

[4] Only occurs on segment 4.

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Twenty-four families were absent from one end of the snag and log gradient. Eight families were restricted to the lower end of the snag and log gradient, with 6 additional families being absent from reaches with the highest snag and log densities (Table 123). Four of these 6 families occurred on $\geq$ 10% of the reaches, including Chrysididae (cuckoo wasps), Acroceridae (small-headed flies), Silphidae (carrion beetle), and Perlodidae (Perlodid stoneflies) was only absent along the snag and log gradient. At the other end of the gradient, 7 families were restricted to higher snag and log densities, with 4 additional families being absent from reaches with the lowest snag and log densities, including Hemerobidae, which was present on $\geq$ 10% of the reaches.

The families shifting in presence along the vegetation gradients were not shared to any substantial degree among vegetation gradients (Table 125). The substantially larger number of families were associated with the upper end of the forest to meadow gradient, reflecting the positive relationship of alpha diversity with meadow, and the negative relationship with mixed conifer. Nine families were restricted to the meadow end of the gradient, with Anthophoridae being present on $\geq$ 10% of the reaches, and an additional 15 families absent from the most forested reaches. Eight of these 15 families were present on $\geq$ 10% of the reaches, most of which ($n = 5$) were not associated with any other gradient: Ephydridae (shore flies), Camillidae (Camillid flies), Corixidae (water boatmen), Sphaeriidae, Calliphoridae (blowflies), Lonchopteridae, Tephritidae (fruit flies), and Pompilidae. Six families were restricted to the forested end of the gradient, including Anthophoridae which was present on $\geq$ 10% of the reaches, with an additional 5 families absent from the most meadow-dominated reaches, including Hemerobiidae which was present on $\geq$ 10% of the reaches.

Along the subalpine vegetation gradient, 7 families were restricted to the lower end of the gradient, with 6 additional families absent from the upper most segment (Table 125). Three of these 6 families were present on $\geq$ 10% of the reaches, including Pompilidae, Hemerobiidae, and Heptageniidae (stream mayflies), which was only associated with the subalpine vegetation gradient. Three families were restricted to the upper end of the subalpine vegetation gradient, with 5 additional families absent from the lowest segment of the gradient, including Clubionidae (two-clawed hunting spiders) which was only absent along this gradient and Acroceridae, which was present on $\geq$ 10% of the reaches.

A similar number of families was associated with each end of the alder–willow gradient (Table 125). Five families were restricted to the lower end of the gradient, with an additional 4 families absent from reaches with the greatest proportion of alder–willow, including Geometridae (frequency of occurrence $\geq$ 10%). Six families were restricted to the upper end of the alder–willow gradient, with 7 additional families absent from reaches with the least alder–willow, including Therevidae (Stiletto flies), Largidae, Hemerobiidae, Silphidae, and Sarcophagidae which were all present on $\geq$ 10% of the reaches. Therevidae was also only absent along the alder–willow gradient.

TABLE 124. Families present on 2 or more reaches and absent from lower or upper segments of each of 4 vegetation gradients. Gradients were defined by principal components analysis. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

Invertebrate family	Forest to meadow gradient low < ---------------- > high				Subalpine vegetation gradient low < ---------------- > high				Alder–willow gradient low < ---------------- > high				Aspen–cottonwood gradient low < --------------- > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Frequency < 10%:																
Arachnida -																
Antrodiaetidae												X	X_1			
Clubionidae[*]							X									
Pholcidae	X_1															
Hexapoda -																
Artematopidae												X				
Bibionidae			X				X				X					
Cerambycidae		X														
Ceratopogonidae			X									X				
Chrysopidae									X_1							
Colletidae				X				X								
Dermestidae				X				X					X			
Dytiscidae				X_4	X											X
Endomychidae					X				X							
Ephemerellidae									X							
Eriosomatidae				X_4	X_1										X	
Eupelmidae						X										X
Hydropsychidae				X						X						
Leuctridae		X														
Lycidae	X															
Melittidae							X									
Melyridae		X													X	
Membracidae												X				
Mymaridae					X											
Nitidulidae	X															X
Pentatomidae				X_4	X											

TABLE 124 cont.

Invertebrate family	Forest to meadow gradient low < ---------------- > high				Subalpine vegetation gradient low < ---------------- > high				Alder–willow gradient low < ----------------- > high				Aspen–cottonwood gradient low < ---------------- > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Frequency < 10%:																
Perlidae															X	
Platygastridae												X				
Polycentropodidae					X											
Psychodidae	X_1														X	
Psychomyiidae									X				X			
Ptilidae		X								X						
Reduviidae			X													
Reduviidae											X					
Rhyacophilidae																X
Saldidae			X				X									
Siphlonuridae														X		
Thripidae														X		
Thyreocoridae				X_4												
Tiphiidae															X	
Trixoscelididae				X_4					X							X
Mollusca -																
Euconulidae	X				X											X
Pisiidae		X										X			X	

TABLE 124 cont.

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Invertebrate family	Forest to meadow gradient low < ----------------- > high				Subalpine vegetation gradient low < ---------------- > high				Alder–willow gradient low < ----------------- > high				Aspen–cottonwood gradient low < ---------------- > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Frequency ≥ 10%:																
Hexapoda -																
Acroceridae							X			X						
Anthophoridae	X															
Camillidae*			X													
Corixidae*			X													
Calliphoridae*			X													
Lonchopteridae			X													
Chrysididae				X												
Tephritidae*			X													
Sarcophagidae			X								X					
Silphidae											X					
Pompilidae			X			X										
Ephydridae*			X													
Heptageniidae*						X										
Therevidae*											X					
Hemerobiidae		X				X					X				X	
Largidae											X					
Geometridae										X						X
Mollusca -																
Sphaeriidae			X													
Summary	6	5	15	9	7	4	4	3	5	4	7	6	3	4	5	7

* Only absent along one gradient.

[1] Only occurs on segment 1.

[4] Only occurs on segment 4.

Finally, the aspen–cottonwood gradient had 7 families restricted to the lower end of the gradient, including Largidae (frequency of occurrence $\geq$ 10%) (Table 125). Five additional families were absent from reaches with the most aspen–cottonwood. Three families were restricted to the upper end of the aspen–cottonwood gradient, with 4 additional families absent from the lowest segment of the gradient. Hemerobiidae, one of the 4 families absent from segment 1, was present on >10% of the reaches.

Ranking Gradients for Beta Diversity
The 8 environmental gradients were ranked to reflect their contribution to beta diversity based on family presence data (Table 126). Alder–willow had the highest total turnover and the highest average Whittaker's index. Channel flow, precipitation, and subalpine vegetation all had the next highest number of total turnovers. The channel flow gradient ranked second highest next to alder–willow because it had the highest number of core turnover, and it had a high average Whittaker's index. Precipitation had the next highest beta diversity, followed by subalpine vegetation. Aspen–cottonwood and elevation were the next highest in total turnover. The remaining 2 gradients had much lower total and core turnovers, as well as Whittaker's index values. The forest to meadow gradient had the lowest number of total turnovers but the highest number of core turnovers, reflecting the positive correlation between richness and this gradient. The combined elevation–precipitation gradient was not ranked in Table 126 because it was redundant with the individual elevation and precipitation gradients, however as a point of comparison it would have ranked below both elevation and precipitation (total turnover = 64, core turnover = 25, β_{wMIN} = 0.148) and among the gradients with the lowest beta diversity.

TABLE 125. Ranking of environmental gradients by their contribution to invertebrate beta diversity based on presence. Data were collected on sample reaches (n = 56) in the Lake Tahoe basin in 1996.

Environmental gradient	Total turnover	Core turnover - freq. ≥ 2 reaches	Average β_{wMIN}	Rank
Alder–willow	81	22	0.188	1
Channel flow	78	27	0.184	2
Precipitation	78	23	0.180	3
Subalpine vegetation	78	18	0.181	4
Aspen–cottonwood	75	19	0.171	5
Elevation	71	28	0.163	6
Snag and log	63	25	0.147	7
Forest to meadow	56	35	0.124	8

Invertebrate Family Turnover by Basin Orientation
Basin orientation can affect family turnover, as did the environmental gradients discussed above. All pair-wise comparisons of orientations were conducted to assess the contribution of basin orientation to family turnover (Table 126). Based on the average β_{wMIN} across all orientation comparisons, orientation contributed substantially to beta diversity compared to the environmental gradients analyzed. Only alder–willow had a higher β_{wMIN} index value. The highest number of turnovers was 30, occurring between north and south, and north and west sides of the basin. The lowest number of turnovers was 21 occurring between east and west sides. It was not possible to compare patterns of family turnover between basin orientation and the other gradients because orientations can not be aligned along a linear gradient, however the

comparison of east–dry and west–wet orientations provides a representation of all orientation comparisons, and the family turnover between these sides of the basin was high ($n = 30$).

Families absent from one or more orientations provide family specific contributions to the gains and losses observed between orientations (Table 127). A total of 60 families (29.6% of all families) were present on more than one reach and were absent from one or more orientations in the basin. A total of 25% ($n = 15$) of the families absent from one or more orientations were present on $\geq$ 10% of the 56 reaches. A similar number of families were absent from each orientation, consistent with the high beta diversity observed among basin orientations. Five families were present in only one orientation: Dytiscidae (predaceous diving beetles, occurring only on the south side), Dermestidae (Dermestid beetles, only occurring on the west side), Membracidae (treehoppers, only occurring on the west side), Ephemerellidae (mayflies, only occurring on the north side), and Pholcidae (cellar spiders, only occurring on the north side). The number of families absent from the north and south sides was the highest ($n = 27$ and 28, respectively), the number absent from the east was the lowest ($n = 19$), and the number absent from the west was slightly higher than in the east ($n = 22$). Of the families present on $\geq$ 10% of the reaches, all but one (Perlodidae) were absent from only one orientation. The percentage of all families absent from one or more orientations that were aquatic or semi-aquatic (28.3%) was approximately 10% higher than their percentage in the population of families sampled (19.2% of all families sampled were aquatic or semi-aquatic). Families occurring on $\geq$ 10% of all reaches and aquatic and semi-aquatic families absent from one or more orientations represent those that may truly be experiencing ecological limits within the basin, as opposed to rare families which may be rare for a variety of reasons.

TABLE 126. Beta diversity index values for invertebrates among basin orientations. The number of families per segment, the number of families only occurring at upper ("gains") or lower ("losses") ends of the gradient, and Whittaker's beta diversity index (β_w) are displayed. A modified version of Whittaker's beta diversity index (β_{wMIN}) is also displayed. N = north, E = east, S = south, W = west side of the basin. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

Basin orientation	Richness of first segment	Richness of second segment	Total richness	Gains	Losses	$\beta_w{}^*$	β_{wMIN}†
N:E	140	149	175	35	**24**	0.200	0.160
E:S	149	141	176	**27**	35	0.216	0.180
S:W	141	142	171	30	**29**	0.211	0.201
N:S	140	141	171	31	**30**	0.217	0.213
E:W	149	142	170	**21**	28	0.174	0.147
N:W	140	142	172	32	**30**	0.223	0.210
average							*0.185*
N and E:S and W	*173*	*171*	*203*	***30***	*32*	*0.178*	*0.178*

 * Whittaker's beta diversity index: $S/\alpha - 1$, where S = total family richness, and α = the average family richness of the two segments being compared.

 † Modified Whittaker's beta diversity index: $(S/s\text{-}max) - 1$, where S = total family richness, and s-max = the highest richness of the two segments being compared, resulting in a minimum beta diversity index value.

TABLE 127. Invertebrate families present on greater than one reach and absent from one or more basin orientations. X's indicate where a family was present. Data were collected on sample reaches (*n* = 56) in the Lake Tahoe basin in 1996.

	Presence by basin orientation			
	Xeric < --- > Mesic			
Invertebrate family	North (*n* = 14)	East (*n* = 14)	South (*n* = 13)	West (*n* = 15)
Frequency < 10%:				
Perlidae	X	X	X	
Ptilidae	X	X	X	
Saldidae	X	X	X	
Tiphiidae	X	X	X	
Bibionidae	X	X		X
Euconulidae	X	X		
Lycidae	X	X		
Melittidae	X	X		X
Nitidulidae	X	X		
Psychodidae	X	X		
Reduviidae	X	X		X
Rhyacophilidae	X	X		
Antrodiaetidae	X		X	
Chrysopidae	X		X	
Hydropsychidae	X		X	X
Melyridae	X		X	X
Polycentropodidae	X		X	X
Siphlonuridae	X		X	
Xyelidae	X		X	
Zonitidae	X		X	X
Artematopidae	X			X
Ephemerellidae	X			
Pholcidae	X			
Cercopidae		X	X	X
Endomychidae		X	X	
Eupelmidae		X	X	X
Gyrinidae		X	X	X
Hahniidae		X	X	X
Thyreocoridae		X	X	
Trixoscelididae		X	X	
Cerambycidae		X		X
Ceratopogonidae		X		X
Clubionidae		X		X
Colletidae		X		X
Mymaridae		X		X
Pisiidae		X		X
Platygastridae		X		X
Thripidae		X		X
Dytiscidae			X	
Eriosomatidae			X	X
Heteroceridae			X	X
Pentatomidae			X	X

TABLE 127 cont.

Invertebrate family	Presence by basin orientation			
	Xeric < --- > Mesic			
	North (*n* = 14)	East (*n* = 14)	South (*n* = 13)	West (*n* = 15)
Frequency < 10% cont.:				
Psychomyiidae			X	X
Dermestidae				X
Membracidae				X
Frequency ≥ 10%:				
Geometridae	X	X	X	
Heptageniidae	X	X	X	
Hesperiidae	X	X	X	
Acroceridae	X	X		X
Anthophoridae	X	X		X
Chrysididae	X	X		X
Hemerobiidae	X	X		X
Sarcophagidae	X	X		X
Vespidae	X	X		X
Perlodidae	X			X
Cleridae		X	X	X
Coenagrionidae		X	X	X
Corixidae		X	X	X
Pompilidae		X	X	X
Silphidae		X	X	X
Sum of absent families	*27*	*19*	*28*	*22*

Concordance Between Diversity Measures

Invertebrate family richness was significantly correlated with all other diversity variables except aquatic family richness (Table 128). Aquatic family richness was not correlated with any other diversity measures, and lepidoptera richness was correlated only with terrestrial family richness and common family richness. Common and rare family richness were correlated with most diversity variables.

Alpha and Beta Diversity

An average of 139.3 (range = 125 to 147, SE = 0.90) invertebrate families were shared among segments (*n* = 20 reaches per segment), based on segment comparisons across the 8 environmental gradients. The average richness lost or gained between segments was 6.7 families (range = 0 to 24, SE = 1.38), and it was significantly greater (based on paired t-test across gradients, t = -9.75, *P* < 0.001) than the average number of family turnovers between segments ($\bar{x}$ = 24.2 families, range = 16 to 30, SE = 0.73). The average number of families shared among segments constituted 68.5% of all families observed, and variation in richness and family turnover constituted 3.3% and 11.8%, respectively, of all families observed.

TABLE 128. Correlations between 5 variables describing invertebrate diversity (richness) in the Lake Tahoe basin. Shaded areas indicate redundant areas of the correlation matrix. Bolded values indicate $P \leq 0.10$. Data were collected on sample reaches ($n = 56$) in the Lake Tahoe basin in 1996.

Diversity variables*	Invertebrate family richness		Lepidoptera genus richness		Rare family richness		Common family richness	
	r	P	r	P	r	P	r	P
Invertebrate family								
Lepidoptera genus	**0.324**	**0.015**						
Aquatic family	0.167	0.218	-0.073	0.592	0.171	0.208	0.148	0.276
Semi-aquatic family	**0.466**	**<0.001**	0.148	0.272	0.216	0.111	**0.481**	**<0.001**
Terrestrial family	**0.981**	**<0.001**	**0.337**	**0.011**	**0.646**	**<0.001**	**0.962**	**<0.001**
Rare family	**0.659**	**<0.001**	0.114	0.402			**0.496**	**<0.001**
Common family	**0.980**	**<0.001**	**0.344**	**0.010**				

* Diversity represented by richness.

The analysis of the relative influence of environmental gradients on gamma diversity in the basin showed that forest to meadow and aspen−cottonwood made the greatest contribution to gamma diversity in the basin (Fig. 50). They were both associated with shifts in 98 families along their lengths, comprising approximately 48% of the total invertebrate family fauna. The diversity associated with the aspen−cottonwood gradient was primarily driven by family turnover, whereas a greater balance of shifts in richness and turnover was associated with the forest to meadow gradient. These 2 gradients were followed in their contribution to diversity by alder−willow, precipitation, and channel flow gradients. Alder−willow had the highest beta diversity of all the gradients, but low alpha diversity, resulting in total shift of only 93 families along its length. The remaining 3 gradients had less than 85 families shifting along their lengths. The difference in compositional change among the gradients ranged as high as 17 families – approximately 8% of the observed total family richness.

The total change in composition was significantly positively correlated with alpha diversity ($r = 0.784$, $P = 0.021$), whereas it was not correlated with beta diversity ($r = -0.378$, $P = 0.356$). The individual contributions of alpha and beta diversity were significantly negatively correlated ($r = -0.871$, $P = 0.005$). In general, net changes in richness (alpha diversity) along gradients were lower but more variable ($\bar{x} = 2.5$, SE = 0.69) than changes in composition (beta diversity) ($\bar{x} = 9.1$, SE = 0.51).
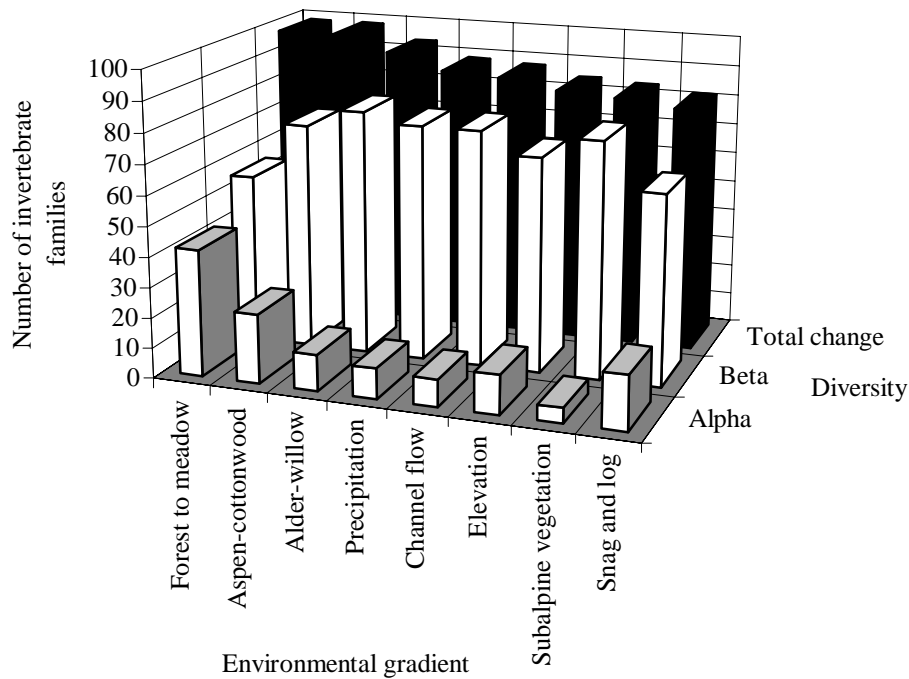
FIG. 50. Contribution of each of 8 environmental gradients to invertebrate family diversity in the Lake Tahoe basin. Total change in composition is shown, along with the composite contributions of alpha and beta diversity. Data were collected on 56 sample reaches in 1996.

Patterns of alpha diversity were relatively consistent between measures of total richness analyzed in the alpha diversity section and calculations of changes in richness between segments along gradients. Invertebrate family richness was positively associated with the forest to meadow gradient, and it had the highest contribution of alpha diversity toward gamma diversity of all the gradients. Invertebrate family richness was also positively associated with alder−willow, but net changes in alpha diversity were low ($n = 12$) along the alder−willow gradient. The strong association of richness with alder−willow was partially the result of increased frequency of occurrence per family along this gradient from lower to upper segments. The average frequency of occurrence of families in each segment went from 4.3 to 4.8 to 5.0 to 5.2 reaches/family from segment 1 to 4, respectively. This indicates that alder−willow is relatively homogeneous and that families that find it suitable habitat will be able to occupy one patch as readily as another, increasing the ubiquitousness of associated families. Aspen−cottonwood and snag and log gradients had some of the highest contributions from alpha diversity toward gamma diversity, but they did not show strong associations with increases or decreases in richness in the analysis of alpha diversity because gains and losses in richness were variable along their lengths.

Environmental Influences on Invertebrate Diversity

Approximately one half of the 500 insect families occurring in California (Powell and Hogue 1979) were detected during sampling in the Lake Tahoe basin in 1995 and 1996. Only 20% of the families encountered were considered aquatic or semi-aquatic even though all sampling was in close proximity to a stream. The number of families shared among reaches was low, with an average of 25% (ranging from 15% to 40%) of all families occurring at any given reach. Alternatively, turnover averaged 12% from lower to the upper half of the 8 environmental gradients examined. Therefore, richness and turnover both contributed substantially to the diversity of invertebrate families, and environmental features that affected alpha and beta diversity all influenced the diversity of invertebrates in the Lake Tahoe basin.

Vegetation was the greatest contributor to the overall diversity of invertebrate families, with meadow, lodgepole pine, alder–willow, and aspen–cottonwood being the top 4 contributors. Channel flow also had a positive influence on invertebrate richness. Turnover associated with changes in channel flow characteristics was low. Despite the steep elevation and precipitation gradients in the Lake Tahoe basin, these variables had limited association with invertebrate family diversity, where only aquatic family richness increased with precipitation and decreased with elevation.

Meadow and lodgepole pine, although occurring on less than half of the sample reaches, had the strongest influence on invertebrate richness of all environmental features assessed. Meadow showed a threshold in its support of invertebrate diversity, where invertebrate family richness increased from a minimum of 25 families where meadow occupied $\leq$ 10% of the reach to a minimum of 60 families where meadow occupied $\geq$ 30% of the reach. Although meadows typically have low structural heterogeneity, approximately 40 more families were associated with reaches with an abundance of meadow (segment 4 on forest to meadow gradient) compared to reaches with an abundance of mixed conifer.

The highest number of families ($n = 12$) with $\geq$10% frequency were restricted to meadow environments, as evidenced by turnover along the forest to meadow gradient. Further, many of these families ($n = 5$) did not show restrictions along any other gradient. Four of these 5 families were in the Diptera order, consisting of various types of flies, including Ephydridae which are shore flies associated with moist environments. The fifth was an aquatic family, Corixidae (water boatman). In summary, it is clear that although the forest to meadow gradient had the lowest beta diversity, there are a relatively high number of unique families, primary Dipterans, uniquely associated with dry and moist meadow environments.

Riparian woodland vegetation (i.e., alder–willow and aspen–cottonwood), in conjunction with meadow, comprised the trio of vegetation types that contributed the most to the diversity of invertebrate families. Richness and turnover had opposing patterns of association with all gradients, and in relation to these top 3 environmental gradients, richness decreased and turnover increased from forest to meadow, to aspen–cottonwood, to alder–willow. Along the aspen–cottonwood gradient, family composition and richness varied primarily as a result of turnover, and richness increased with increases in aspen–cottonwood, particularly the richness of rare families. Aspen–cottonwood provides a rich array of resources and support a unique array of invertebrate families.

The amount of alder–willow occurring on a given reach considerably affected the composition of invertebrate families. And although many measures of invertebrate richness (i.e., total richness, semi-aquatic, and terrestrial groups) increased with increases in alder–willow, the number of families gained along the alder–willow gradient was relatively low (average of 12 families gained per segment). This apparent contradiction was the result of a greater frequency of occurrence per family associated with upper segments of the alder–willow gradient. These results suggest that alder–willow provides a set of unique physical structures and an array of resources, but homogeneous environment, that provides habitat for a unique assemblage of families.

Channel flow was the most influential non-biotic environmental feature associated with invertebrate family diversity. Richness, as reflected in many measures (total richness, richness of both frequency classes, aquatic and terrestrial group richness), increased with channel flow. Aquatic family richness increased uniquely with channel width. Meadows occupied the highest percentage of each

reach where channel flow was lowest ($\bar{x}$ = 19.7%, SE = 0.06 for channel flow segment 4), and the proportion of meadow occupying each reach increased with decreases in channel gradient. These relationships suggest that low gradient channels are associated with more open-canopied environments and they have greater access to floodplains, which in turn increases stream productivity and the development of riparian-associated vegetation (Gregory et al. 1991).

Orographic effects on invertebrate family composition were substantial. The large numbers of families absent from one or more orientations (ranging from 19 to 28 per orientation) far exceeded the number observed for any of the environmental gradient segments, with a subset of 13 families being absent from 2 adjacent orientations. Of the 15 families with frequencies ≥ 10% that were absent from one or more orientations, 4 were aquatic: Heptageniidae (stream mayflies; missing from the west side), Perlodidae (common stoneflies; missing from east and south sides and highest snag and log densities), Corixidae (water boatman; missing from the north side and lowest elevations), and Coenagrionidae (narrow-winged damselflies; missing from the north side).

Since the majority of invertebrates are highly mobile, I would not expect the topographic features of the Lake Tahoe basin to be barriers to dispersal. Of the vegetative features most associated with invertebrate richness (meadow, alder–willow, and lodgepole pine), only lodgepole pine varied by orientation. Physical characteristics varied considerably among orientations, with precipitation and channel width varying most significantly. Although total richness did not vary by orientation, aquatic family richness was higher on more mesic south and west sides (compared to the north and east sides) of the basin. Here it appears that the unique influence of precipitation and channel width on aquatic family richness is being expressed and is primarily responsible for the shifts in composition among orientations.

Individual Families and Family Groups

The investigation of family groups defined by environmental association and frequency of occurrence was helpful in discerning environmental features of relevance to these important subsets of species. Associations of total richness were driven largely by common and terrestrial families, and the unique associations of rare and aquatic families were not strongly expressed in this composite measure. Aquatic and terrestrial family groups were both closely associated with environmental variables, with few shared associations. As observed for total family richness, aquatic and terrestrial family groups were positively correlated with channel flow, with gradient being the most influential channel flow element. Other than this commonality, aquatic family richness was more governed by abiotic conditions (higher richness at low elevations and high precipitation) and terrestrial family richness was more governed by vegetative conditions (higher in association with riparian and meadow vegetation as opposed to forested conditions). The semi-aquatic family group was only associated with alder–willow.

The identification of frequency classes assisted in the ecological interpretation of overall patterns of invertebrate richness. Rare families were more speciose in association with meadows, and were likely to be largely responsible for the positive association between invertebrate richness and meadows, and the negative association between invertebrate richness and snags and logs. Common families were more speciose in association with alder–willow vegetation, and were likely to be largely responsible for the positive association between invertebrate richness and alder–willow. In relation to physical features, common families are probably responsible for the positive relationship observed between richness and low gradient, slow flowing streams, with gradient being the most consistently associated with richness.

Lepidoptera genus richness was positively correlated with many other richness measures (total family richness, common family richness, and terrestrial family richness), but to a lesser degree than these measures were correlated with one another. Virtually no relationships were observed between the richness of Lepidoptera genera and the environmental features described in this study. The strong environmental relationships observed for invertebrate richness contrasted with the weak environmental relationships observed for lepidoptera richness indicate that lepidoptera genera are not good indicators of overall invertebrate richness in the Lake Tahoe basin.

The alder−willow gradient had the greatest number of frequently occurring families restricted to one portion of its length compared to the other 7 environmental gradients. Seven families with frequencies $\geq$ 10% were absent at one or the other end of the alder−willow gradient: Geometridae, Acroceridae, Therevidae, Hemerobiidae, Pompilidae, Sarcophagidae, and Largidae. Geometridae and Acroceridae were absent from reaches with the greatest amount of alder−willow. Geometridae, commonly known as the inch worm family, is a large family in the Lepidoptera order. Inch worms, the larval form of the moths, typically feed on the foliage of deciduous trees. Geometers may not find alders and willows particularly palatable or the alder−willow community may be too homogeneous to support the foraging needs of this family. Acroceridae, small-headed flies in the Diptera order, are internal parasites of spiders in their larval stage, and some species of the family feed on flowers in the adult stage, while in other species the adults do not feed (Borror et al. 1989).

Five families were absent from reaches with the least alder−willow: Therevidae (stiletto flies), Hemerobiidae, Pompilidae, Sarcophagidae (flesh flies), and Largidae (largid bugs). These families may be dependent on alder−willow, particularly Therevidae, which was relatively common (occurred on 18 of the 56 reaches) and only associated with the alder−willow gradient. Therevidae are commonly found in dry open areas such as meadows (Borror et al. 1989). The larvae are predaceous and usually occur in sand or decaying wood, and the adults are believed to be plant feeders (Borror et al. 1989). The adults may find alder−willow communities ideal habitat. Pompilidae are spider wasps in the bee superfamily (Apoidea) and the Hymenoptera order which feed on spiders as larvae, and the nectar of flowers as adults. Hemerobiidae are brown lacewings in the Neuroptera order which are generally found in wooded areas (Borror et al. 1989). Eggs are laid on plants and larvae and adults are predaceous feeding on small insects primarily (Borror et al. 1989). Sarcophagidae are flesh flies in the Diptera order. Adults feed on plant materials, but the larvae generally feed on animal material of some kind. Relatively little is known about the habits of the Largidae, a bug family in the Hemiptera order.

Along the channel flow gradient, 28 families were associated with only the lower or upper end of the channel flow gradient. The number of families restricted to each end of the channel flow gradient were relatively equivalent in number, but many more of the families with frequencies $\geq$ 10% were missing from the lower end of the gradient. Lonchopteridae, Silphidae, and Largidae were present on $\geq$ 10% of the reaches and missing from the lowest segment. Lonchopteridae (spear-winged flies), was associated with only channel flow and the forest to meadow gradient (missing from segment 1). Lonchopteridae commonly occur in moist, shady or grassy environments such as riparian areas (Borror et al. 1989). Only 4 species occur in this family in North America. Silphidae are carrion beetles, and most species feed on dead animal material as larvae and adults. Largidae was also missing from the highest elevation and the lowest segment of alder−willow, as well as the lowest segment of the channel flow gradient.

Of the remaining 25 families absent from one end of the channel flow gradient, none were uniquely associated with this gradient. However, Rhyacophilidae (primitive caddisflies) was found only in association with the lowest channel flow, and 3 additional families were found in association with only the highest channel flow: Dytiscidae (predaceous diving beetles), Membracidae (treehoppers), and Pentatomidae (stink bugs). The frequency of occurrence of these families was too low to speculate as to the potential ecological significance of their association with channel flow; however most of them are specialists in some manner (e.g., treehoppers feed on specific tree or shrub species) (Borror et al. 1989).

A total of 18 families were associated with only one end of the subalpine vegetation gradient, but only Heptageniidae (stream mayflies) was present on $\geq$ 10% of the reaches. Heptageniidae was only absent along the subalpine vegetation gradient, and was absent from the upper most segment of the gradient. Heptageniidae, a member of the Ephemeroptera order, is the second largest family of mayflies in North America. A total of 4 families in this order were detected, but only the presence of this one family appeared to be associated with the subalpine vegetation gradient. Most species in the Heptageniidae occur on the underside of stones in streams, but some occur in sandy rivers (Borror et al. 1989). Mayfly eggs are laid on the surface of the water or are attached to objects in the water. Larvae feed on small aquatic organisms and organic debris (Borror and White 1970), and often emerge as adults in pulses (Borror et al. 1989). Mayflies provide a valuable food source for fish, amphibians, birds, spiders, and some predaceous insects (Borror et al. 1989).

Two other families (Clubionidae and Eriosomatidae) with low frequencies ($n = 3$ reaches each) were restricted to the upper or lower most segments of the subalpine gradient. Clubionidae are two-clawed hunting spiders of the Arachnida order which occur in foliage or on the ground, and Eriosomatidae are wooly and gall-making aphids of the Homoptera order which feed on plants and serve as prey for many other species of invertebrates. The frequency of occurrence of these 2 families was too low to speculate on their ecological associations.

The aspen–cottonwood gradient had 19 families absent from either extreme of the gradient, but only one, Geometridae (inchworm), was present on $\geq$ 10% of the reaches. Geometridae was absent from the lowest segment of aspen–cottonwood gradient. Geometridae was also absent from the highest elevation reaches, and reaches with the most alder–willow. It is likely that aspen provides a highly palatable food source for inchworms in the Lake Tahoe basin. Inchworms are known to feed upon the leaves of aspen and can severely defoliate aspen stands under certain circumstances (Furniss and Carolin 1977).

Only one family with a frequency $\geq$10% was missing from $\geq$ 2 orientations: Perlodidae ($n = 7$) (common stonefly of the Plecoptera order) was missing from east and south. Six other families from the Plecoptera order were detected in the study area, and only one other, Perlidae ($n = 5$), showed any pattern of association with orientation. Perlodidae are common in cool, clear streams, and the north and west sides of the basin had the highest elevation stream reaches in the study area. It is possible that stream temperature had some part to play in the distribution of Perlodidae.

Conservation and Management Implications

California has a rich and diverse insect fauna, and may have the largest percentage of endemic insect species in America north of Mexico (Kimsey 1996). Thirty-one orders of insects occur in California, representing approximately 500 families. An estimated 250 species of butterflies occur in California (Robbins and Opler 1997), and 155 of these species (representing 7 families) are estimated to occur in the Sierra Nevada (Shapiro 1996). Aquatic invertebrates are also diverse, although their richness and composition in the Sierra Nevada are less well known (Erman 1996). The number of families detected in this study was substantial, however direct comparisons with other studies are difficult because few studies span the range of taxa and environments encompassed by this study, and most studies assess richness and composition at the species level.

The high diversity of invertebrate families, their close association with vegetation, and the dual contributions of richness and turnover indicates that the quality and diversity of vegetative conditions would be critical to the conservation of invertebrates. Conservation of invertebrate diversity would require areas large enough to support the richness of the site, and many sites such that representatives were identified for the full diversity of vegetation types, emphasizing meadow and riparian woodland vegetation types and lower elevation areas.

Researchers commonly report variation in the composition of invertebrates among different biotopes (e.g., Thomas and Mallorie 1985, Bedford and Usher 1994), and variation in that richness in association with plant species richness (e.g., Tilman 1982, Thomas and Mallorie 1985) and vegetation complexity (Lawton and Strong 1981, Gardner et al. 1995). For example, Thomas and Mallorie (1985) surveyed a variety of forested, shrubland, and meadow biotopes for butterflies and also found that richness was highest in meadow environments, specifically where vegetation height was 5 to 25 cm. Gardner et al. (1995) found that arthropod diversity was lower on sites with reduced vegetation complexity along a grassland to forest gradient in Argentina. However, most studies address invertebrate diversity within a single biotope (e.g., Golden and Crist 1999, Panzer and Schwartz 1998) or a narrow taxonomic group (e.g., Bedford and Uster 1994, Kremen 1994). Further, not all of those addressing multiple biotopes have observed differences in invertebrate richness among vegetation types (e.g., Rykken et al. 1997, re: carabid beetles), suggesting that the influence of vegetation structure and composition can vary dramatically by the taxonomic groups and biotopes studied.

The strong role of vegetation types in my study, particularly meadow and riparian woodland types, in supporting a diversity of invertebrates in the Lake Tahoe basin has important management implications. Most importantly, the management of meadow and riparian vegetation supports not only aquatic and semi-aquatic invertebrates, but a wide range of terrestrial families as well. Channel restoration projects can potentially have the greatest influence on these vegetative conditions.

Channel restoration efforts are relatively common (TRPA 1997), and their impacts on riparian and meadow vegetation should be considered in light of their importance to invertebrate diversity.

Meadows and grasslands are considered highly productive environments and are commonly associated with rich invertebrate assemblages (Curry 1994). High radiant energy associated with lack of an overstory may be influencing the richness of invertebrates associated with meadows as much or more than the vegetation itself (e.g., Li et al. 1994, Jacobson et al. 1997). Invertebrates are heterotherms and depend on external heat sources to function. The indication of an ecological threshold for meadow, although based on a modest sample size (n = 9 reaches with $\geq$ 30% meadow), suggests that meadows serve an important role in the support of invertebrate diversity in the Lake Tahoe basin. Similarly, one or more rare families was consistently present where any meadow ($\geq$ 1%) occurred in the sample reach. The presence of some meadow appears to greatly enhance the richness of invertebrate families, and thus meadow management should be a primary element in any strategy for the conservation of invertebrate diversity in the basin. Conversely, invertebrate diversity should be considered in the management of meadows.

Thresholds observed for invertebrate family richness in relation to the amount of meadow corroborate the results of other studies showing that resources associated with meadows (e.g., food, cover, nest sites) may reach necessary levels of abundance or diversity only in meadows above a certain size or extent (e.g., Bowers 1986, Linusson et al. 1998, Wettstein and Schmid 1999). The greatest threats to meadow condition and extent are lack of fire, which can affect succession, and water diversions and grazing, which can affect the hydrodynamics and plant diversity of meadows (Ratliff 1985). Agencies within the Lake Tahoe basin are increasing the use of prescribed fire in an attempt to restore the function of fire in reducing flammable fuels. Prescribed fires and wildfires that are allowed to burn should generally improve the plant diversity and extent of meadows in the basin. Water diversions are rare in the basin, but channel restoration efforts should consider potential impacts on meadow systems. Most meadows in the basin are currently grazed by cattle, and only a few allotments exclude cattle from grazing adjacent to stream channels (USDA 1988). Grazing may have a deleterious effect on plant species composition, diversity, and flower production if over-grazed (e.g., Fleischner 1994).

It appears that aspen–cottonwood provides unique resources (type, quality, or quantity) which contribute substantially to the richness of invertebrates in the Lake Tahoe basin and provide habitat for less frequently observed families which may be rare in the basin. Furniss and Carolyn (1977) listed 33 insect species that use aspen as a food source, including (but not limited to) members of the Tortricidae (tortrix moths), Lasiocampidae (tent caterpillars), Geometridae (inch worms), Cicadellidae (leafhoppers), Cerambycidae (long-horned beetles), and Noctuidae (noctuid moths). Aspen communities are considered highly productive environments because of their high insect populations and the high food value associated with their catkins, buds, and leaves (Brinkman and Roe 1975, Verner 1988). Given that aspen–cottonwood represented a relatively weak vegetation gradient, its strong association with diversity suggests that it may function as a sort of "keystone" resource (e.g., Daily et al. 1993, Power et al. 1996) for the gamma diversity of invertebrates in much the same manner as that discussed for bird diversity (see Chapter 5). As such, it would be ideal to manage aspen for biological diversity. Aspen stands are sometimes ephemeral vegetation associations which are succeeded by conifer forests in the absence of fire. However, depending on soils and moisture, some aspen stands can be relatively permanent features even in the absence of fire (Barry 1971, Youngblood and Mueggler 1981, Mueggler and Campbell 1982). In the Lake Tahoe basin, it is possible that the lack of fire has reduced the extent of aspen. The increased use of prescribed fire and proportion of wildfires that are allowed to burn are likely to improve the vigor and perhaps the extent of aspen stands in the basin.

Given the high richness and turnover associated with alder and willow vegetation, a range of densities of alder and willow would probably provide habitat for a greater number of families than would be accommodated by high densities of alder–willow. Alder–willow is considered a highly productive environment (Grenfell 1988) and both alder and willow have many specific and non-specific invertebrate predators. Alder and willow occurred frequently along stream reaches, and was generally well distributed throughout the Lake Tahoe basin. Management activities are unlikely to change the distribution of alder and willow, however grazing and channel restoration could alter its

abundance. In particular, channel restoration could affect alder and willow abundance, as well as meadow conditions. Restoration efforts that involve key meadow complexes with well developed alder and willow vegetation should be carefully considered so as to avoid detrimental effects on riparian and meadow vegetation and habitats for invertebrates.

In general, conifers did not provide for high diversity of invertebrate families. Invertebrate richness showed a negative relationship with mixed conifer forests and no relationship with subalpine conifer forests. The negative relationship with mixed conifer is most likely a function of its juxtaposition with meadow at low to mid elevation sites. In addition, few unique species were associated with mixed conifer, as evidenced by the low turnover associated with the forest to meadow gradient. However, as established by other studies, many invertebrates are most frequent and abundant in evergreen forest vegetation types, and these vegetation types are important in the maintenance of such species in the Lake Tahoe basin. Thus, conifer vegetation types serve to support a small proportion of unique invertebrate families and their management may have negligible effects on the richness of invertebrate families in the basin. It is likely that unique associations are more prevalent at the genus and species level, and that the management of conifer vegetation would affect diversity at these lower taxonomic levels.

The snag and log gradient was negatively associated with invertebrate family richness, a relationship that was driven primarily by terrestrial and rare families. It is likely that the negative association of invertebrate richness with snags and logs is in part an indirect reflection of the strong positive association between richness and meadows (which have low snag and log densities). However, woody debris is an important substrate and food source for many invertebrate taxa (Emerson and Jacobson 1976, Price 1984, Borror et al. 1989), as evidenced by the 7 families restricted to the upper end of the snag and log gradient. These 7 families could be greatly affected by forest management that greatly reduces snag and log densities.

A high density of small snags and logs occur in the Lake Tahoe basin as a result of recent large-scale tree mortality events (Weatherspoon et al. 1992, McKelvey et al. 1996, Manley et al. 2000), as evidenced by the high frequency of occurrence (> 80%) of large snags and both sizes of logs across all sample reaches. Attempts to reduce fine fuels in the basin may reduce the density of small snags and logs, but may also pose a risk to the quality and quantity of large snags and logs. Charring can reduce the suitability of snags and logs as foraging substrates or cover for invertebrates. Careful fire management to conserve the quality and quantity of large snags and logs would contribute to retaining valuable habitat elements for forest-associated invertebrates.

The positive affect of channel flow on invertebrate diversity and the relatively high turnover along the channel flow gradient points toward careful consideration of invertebrates in the management and restoration of stream channels in the Lake Tahoe basin. Ormerod et al. (1994) found a turnover in species composition along 2 rivers in Nepal. Many channel features changed along the rivers, including elevation. They found that few taxa were restricted to upper reaches of the watershed, but many only occurred in lower reaches. Li et al. (1994) found that environments that were open-canopied or lacking an overstory were associated with higher invertebrate biomass in streams in Oregon, owing potentially to increased radiant energy. Only aquatic family richness increased in concert with channel width, and thus low-gradient, wide channels may provide special habitats and conditions for aquatic invertebrates which facilitate their higher richness. The assemblages of families associated with wide streams and their environmental requirements and sensitivities should be considered in restoration activities regardless of their location in a watershed. Consistent with the river continuum concept (Vannote et al. 1980), Ormerod et al. (1994) found that the most abundant taxa shifted from filters feeders (e.g., Baetidae [mayflies]) at upper reaches to burrowers and pool dwellers (e.g., Hydropsychidae [net spinning caddisflies], Simuliidae [black flies]) at lower reaches. These shifts in life history strategy from headwaters to mouth have not been demonstrated to occur in small mountain watersheds, however my results suggest that some magnitude of transition is occurring, at least in composition. Further study could provide valuable insigOrmerod et al. 1994). Globally, higher precipitation is usually accompanied by higher insect species richness (e.g., Brown and Davidson 1977), however patterns of precipitation are typically accompanied by other potentially equally influential factors, such as climate stability, temperature, and plant species diversity (Price 1984). In this study, elevation and precipitation had a minor influence on the richness of invertebrate

families, but they did affect aquatic invertebrate richness. Jacobsen et al. (1997) found that the richness of aquatic invertebrate families decreased with elevation, in conjunction with decreases in water temperature. Similarly, Ormerod et al. (1994) found higher richness of aquatic invertebrate families at lower elevations. Although forest management does not affect elevation and precipitation, it is important to note that the richness of aquatic invertebrates will be more greatly affected at lower elevation sites, particularly in areas of higher precipitation such as the west side of the basin.

Strong environmental relationships were observed for invertebrate family richness. This suggests that the resolution of diversity and environmental variables were compatible. Other researchers have successfully addressed invertebrate diversity by analyzing family richness (e.g., Ormerod et al. 1994, Gardner et al. 1995, Jacobson et al. 1997, Bailey et al. 1998). My results indicate that addressing diversity at the family level could be a tenable option for monitoring invertebrate diversity at geographic scales as large or larger than the Lake Tahoe basin (> 100,000 ha).

The inverse relationship observed between alpha and beta diversity is probably a function of assessing invertebrate richness at the family level. Most invertebrate families (particularly the terrestrial ones) encompass a high number of species with varying habitat associations. It is likely that turnover in species composition along these gradients is high, because as richness increases, the probability of the same family occurring in opposing biotopes or habitat conditions would be greater than for the same genus or species. However, Tockner et al. (1999) found that the alpha diversity and beta diversity of molluscs and odonates (as well as macrophytes) described at the species level also showed an inverse relationship to one another in regard to channel connectivity. Studying patterns of invertebrate richness at a variety of taxonomic levels, including family, genus, and species levels, would provide more ecologically-based relationships between alpha and beta diversity by revealing the differential rate of turnover among taxonomic levels. Once established, shifts in higher taxonomic levels along key environmental gradients may serve as strong indicators of lower level shifts in richness and composition.

The inclusion of spider families in the calculation of invertebrate richness greatly broadened the phylogentic diversity of invertebrate taxa. Increasingly, spiders are being considered for use as indicator taxa as measures of diversity and indicators of environmental conditions (e.g., Pettersson et al. 1995, Oliver and Beattie 1996b). Although a high level of expertise is needed to identify spider species, the use of morphospecies as a metric of richness has promise as a strong indicator of the biological diversity of spiders (e.g., Oliver and Beattie 1996b).

Butterflies have been suggested as potential indicators of the diversity of other taxa, including other invertebrates and vertebrates (e.g., Murphy and Wilcox 1986, Erhardt and Thomas 1991, Sutton and Collins 1991, Kremen 1992, Daily and Ehrlich 1995, Nelson and Epstein 1998). They are considered potentially strong indicators for a variety of reasons, such as: (1) they are generally easy to identify and the taxonomy is fairly well developed; (2) they are sensitive to environmental changes at a range of spatial scales because individually they are often highly plant specific (Ehrlich and Raven 1964, Pullin 1995), but as group they rely on a variety of plant species; and (3) most species fly as adults for much of the dry season, reducing the possibility of missing a substantial portion of the fauna because of mis-timed sampling (Daily and Ehrlich 1995). For example, Kremen (1992) found a strong correlation between plant species richness and total abundance in the butterflies of Madagascar. The lack of associations observed between Lepidoptera genus richness and environmental features contrasts with the strong relationships observed for invertebrate family richness , and suggests that Lepidopera diversity does not serve as a reliable indicator of invertebrate diversity in the Lake Tahoe basin. It is possible that the richness of Lepidoptera species would show a stronger relationship with the richness of other invertebrate taxa, or that a stronger relationship would exist if Lepidoptera genera were being correlated with the richness of invertebrates at the genus level. These findings serve to emphasize the need to establish cross-taxonomic relationships in each environment in which they are to be applied before relying on indicators to assess diversity. hts into the occurrence and form of longitudinal succession occurring in the Lake Tahoe basin.

The diversity of invertebrates was expected to follow the general trend of decreasing diversity with elevation and increasing trend in relation to precipitation (e.g., Kremen 1994, Ormerod et al. 1994). Globally, higher precipitation is usually accompanied by higher insect species richness (e.g., Brown and Davidson 1977), however patterns of precipitation are typically accompanied by other

potentially equally influential factors, such as climate stability, temperature, and plant species diversity (Price 1984). In this study, elevation and precipitation had a minor influence on the richness of invertebrate families, but they did affect aquatic invertebrate richness. Jacobsen et al. (1997) found that the richness of aquatic invertebrate families decreased with elevation, in conjunction with decreases in water temperature. Similarly, Ormerod et al. (1994) found higher richness of aquatic invertebrate families at lower elevations. Although forest management does not affect elevation and precipitation, it is important to note that the richness of aquatic invertebrates will be more greatly affected at lower elevation sites, particularly in areas of higher precipitation such as the west side of the basin.

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